LAKEWARD AND DOWNSTREAM MOVEMENTS OF AGE-0 ARCTIC GRAYLING (*THYMALLUS ARCTICUS*) ORIGINATING BETWEEN A LAKE AND A WATERFALL

Mark A. Deleray[1] and Calvin M. Kaya[1,2]

ABSTRACT—Arctic grayling in Deer Lake, Montana, spawn only in the 350-m segment of outlet stream between the lake and a waterfall. The purpose of this study was to examine consequences of and possible adaptations by this population to spawning above the falls, by determining the extent of loss over the falls of age-0 young, the daily and seasonal patterns of such losses, and the seasonal pattern of movement upstream into the lake by the remaining young. We measured fish movements during 1989 and 1990 with traps placed at the outlet and at the falls, from fry swimup in July until October or November. Young went over the falls predominantly as newly swimming fry at night. In 1989 about 5000–9000 were lost downstream, representing an estimated 4–7% or less of young produced. Most young thus appear adapted to maintaining their position above the falls. A few started entering the lake in August and September, but only 95 in 1989 and 23 in 1990 had done so by the time observations were ended by the onset of wintery conditions. Most movement into the lake appeared to occur sometime during the six to seven months of annual ice cover. This extended period of stream residence contrasts with early lakeward movements reported for other inlet-spawning, lacustrine grayling populations and may be an adaptation for avoiding predation by large conspecifics in Deer Lake.

Key words: *migration, fish, grayling,* Thymallus arcticus, *salmonids, waterfall, stream, lake.*

Limited information is available on movements of young fish from populations inhabiting or spawning in small headwater streams above waterfalls. An innate tendency of young fish from such populations to hold position or move upstream in water current (positive rheotaxis) would be highly advantageous in preventing their irretrievable loss over the falls. Such loss should be limited to enable the population to maintain itself, and appropriate behavioral adaptation would be promoted through removal from the gene pool of young fish that did go downstream. Evidence for such adaptation is provided by studies reporting little or no loss over waterfalls of young fish from long-established, native populations of rainbow trout (*Oncorhynchus mykiss*) and cutthroat trout (*O. clarki*) in North America (Northcote 1969, Northcote and Hartman 1988) and brown trout (*Salmo trutta*) in Europe (Jonsson 1982). Experimental studies have provided evidence for a genetic basis of such rheotactic adaptation in rainbow trout and brown trout (Northcote 1981, Northcote and Kelso 1981, Jonsson 1982).

Although there is evidence for genetically based, positive rheotaxis by young Arctic grayling (*Thymallus arcticus*) in streams (Kaya 1989, 1991), there have been no previous studies on their possible loss over waterfalls. Young grayling may be more susceptible to such loss than young trout, since young grayling are much smaller and appear to be weaker swimmers. At swimup (initiation of swimming), young grayling are about 9–11 mm in length (Kaya 1991), compared to 20 mm or more for rainbow trout (Northcote 1962). The present observations were conducted on a population of grayling that lives in a lake near the head of a mountain valley and spawns only in a short stream section between the lake outlet and a waterfall. Objectives of the study were to determine whether age-0 (first-year) young are lost downstream over the falls, the daily and seasonal patterns of such losses, and the seasonal patterns of their upstream movement into the lake. Perpetuation of such a population would depend on limited downstream loss of their progeny, and residence in the lake would require upstream migration by the young. The study was designed to include movements of the earliest mobile larvae, an

[1] Biology Department, Montana State University, Bozeman, Montana 59717
[2] Author to whom correspondence should be addressed.

aspect that appears lacking from most past studies involving downstream movements from salmonid populations above waterfalls.

STUDY SITE AND POPULATION

Observations were conducted in 1989 and 1990 on the 350-m long section of Deer Creek that flows from Deer Lake to a 3-m, vertical waterfall. The lake is located at 2780 m altitude near the head of a mountain valley in the Madison Range of southwest Montana. Dimensions of the stream on 19 August 1990, measured bank-to-bank at five locations along each of 34 transects between the lake outlet and the waterfall (Deleray 1991), were mean width of 5.88 m (range 1.08–21.0), mean depth of 0.10 m (range 0.0–0.41), and mean water velocity (measured at 0.6 × depth at each location) of 0.05 m/sec (range 0.0–0.48). Estimated discharge volume ranged from about 0.02 to 0.05 m^3/sec between 2 July and 9 September 1990.

Previous observations had indicated that Arctic grayling, the only fish in the lake, spawn only in the outlet stream (Kaya 1989). The outlet stream is inhabited by grayling fry (age-0 fish smaller than about 2.5 cm in length; Piper et al. 1982) and other young up to about 14 cm in length. Larger fish are rare, except when spawning adults are present during early summer. Numbers of adults spawning in the stream were estimated by electrofishing mark-and-recapture methods at 803 (95% CL ±104) in 1989 and 1109 (95% CL ±124) in 1990, with similar numbers of males and females (Deleray 1991). The 350-m segment between the lake and the waterfall is the only part of Deer Creek inhabited by grayling. Near the base of the waterfall the stream disappears beneath the surface of a steep talus slope before reemerging about 200 m downslope. Grayling are not present in the 10 km of stream between the lake and the Gallatin River, perhaps because of the stream's steep gradient (about 1000 m/10 km) and numerous cascades. Fish habitat is absent upstream from the lake, and the population is thus physically isolated within the lake and the short section of stream above the waterfall.

METHODS

Methods and observation schedules were influenced by the relatively remote location of the study site. The lake is located within a designated wilderness area and is reached via a trail that extends about 10 km from and climbs about 1000 m above the nearest motor vehicle access. Loss of ice cover from the lake and stream and spawning activities by grayling were monitored through weekly hikes to the site starting in late May. Observations of fish behavior started as the ice thawed and adults began entering the stream, mid-June in 1989 and late June in 1990, and ended as ice started forming on the lake and stream margins (10 November 1989) or as snow accumulations on the trail made access difficult (11 October 1990). Stream temperature was continuously recorded throughout both observation seasons with a Peabody Ryan Model D thermograph placed about 30 m downstream from the lake. Daily mean temperature was calculated as the average of daily maximum and minimum.

Traps with 1-mm-mesh netting were placed to determine the dates fry became free-swimming, and to monitor their movement downstream and upstream out of the outlet stream. In 1989 three fry emergence traps (45 × 45 cm) of the type described by Fraley et al. (1986) were placed over the substrate after most spawning had ceased, over areas where fish had been seen spawning and where concentrations of eggs were visible. Because Arctic grayling spawn over the substrate without excavating redds, eggs were readily visible among the substrate particles. One emergence trap was placed in a spawning area about 30 m below the outlet, and the other two were placed in the principal spawning area about midway through the stream length. Swimup fry in the traps were removed and tabulated daily or on alternate days until emergence ceased.

One-way traps were placed across the lake outlet and at the top of the waterfall to monitor movement of young out of the stream. The upstream trap had V-shaped, screened barriers extending completely across the outlet and leading upstream into a holding box. This trap retained fish as they entered the lake. The trap was installed after most adult spawners had left the stream but before the young became free-swimming. After installation, the trap was in continuous operation through both observation seasons. It was inspected at intervals varying from several days to about one week; young were removed, measured, and released upstream into the lake.
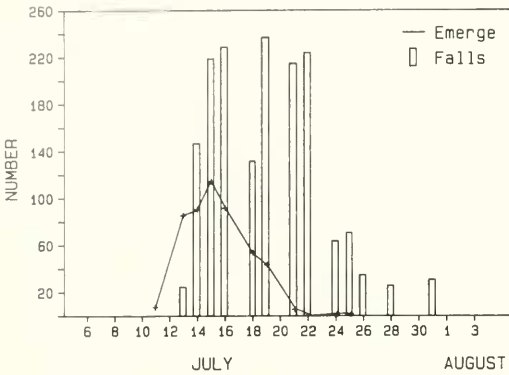
The downstream trap was a drift net with its

Fig. 1. Total number of young Arctic grayling (*Thymallus arcticus*) in three emergence traps placed over the substrate, and in the waterfall trap, Deer Creek, Montana, 1989.

opening positioned at the lip of the waterfall; it collected young that were going over the falls. In 1989 this trap sampled about 0.3–0.5 of the stream volume, as estimated by comparing flow rate into a plastic sack attached to the trap versus estimated stream discharge volume. In 1990 V-shaped barriers were added to direct all flow through the net. In 1989 the trap was installed on sampling days and left in place for about 24 h before the young within were tabulated and measured. The trap was deployed on 6 July, before fry became free-swimming, and operated at intervals of one to two days until numbers in the trap declined sharply. Thereafter, the trap was operated at intervals of several days to two weeks until 19 October. In 1990 this trap was operated less frequently, at intervals ranging from five days during the swimup period to about four weeks in September and October, to determine diel patterns of movement over the falls of young at different ages post-swimup. Sampling began on 23 July as fry started to swim. On sampling dates the trap was deployed at 1000 or 1100 h (Mountain Standard Time); the trap was emptied of young at 1400 h, and thereafter every 4 h until 1000 h the next day.

RESULTS

Spawning occurred through much of the 350-m length of the stream, from about 10 m below the lake outlet to within 15–20 m of the falls. The most heavily used area was a 10-m reach about 130–140 m above the falls. In 1989 spawning occurred during the last week of June, and swimup of fry in the emergence traps began

about 11 July, peaked in mid-month, and continued until about 25 July (Fig. 1). Spawning in 1990 occurred during the first week in July, and swimup of fry began in mid-month and continued to the end of the month.

In 1989 fry started appearing in the falls trap as they became free-swimming (Fig. 1). Highest daily totals of fry in the falls trap, generally over 200 per day, occurred 15–22 July as numbers of fry becoming free-swimming in the emergence traps peaked, and then declined. The swimup period ended about 25 July; thereafter, within a week, numbers of young in the falls trap declined to 0–6 per day. No young entered the falls trap after 20 September.

Movement of fry over the falls was concentrated within a 19-day period, 13–31 July. The falls trap was operated for 13 of these days, and the mean number of fry per 24-h sample was 127.3. Extrapolation from the estimated 30–50% of total stream volume that passed through the net, and application of the 13-day mean to 19 days, yielded a crude estimate of 4837–8062 young grayling lost over the falls 13–31 July. Numbers in the falls trap averaged only 2.7 per day during the 11 days sampled from 1 August to 20 September, the last day young entered the trap. Similar extrapolation to this 51-day period yielded a crude estimate of an additional 275–459 young lost. Thus, the number of young lost downstream over the falls in 1989 during the period from swimup of fry to onset of ice cover over the stream was roughly estimated at 5000–9000.

Fry were already becoming free-swimming when the falls trap was installed on 23 July 1990. Numbers of young per day in the falls trap peaked at 561 on 28 July, diminished to 49 ten days later on 6 August, and to 5 by 8 September. No young entered the trap on 12 October, the last day sampled in 1990. During the swimup period fry went over the falls predominantly at night (23 and 28 July; Fig. 2). However, there was no consistent pattern of diurnal vs. nocturnal movement among the fewer young fish that went over the falls on later dates (6 and 17 August; Fig. 2). Too few days were sampled at the falls in 1990 to estimate total numbers lost.

In contrast to early losses over the falls, upstream movement of young grayling into the lake did not begin until late summer, when the fish were larger and water temperatures were cooling (Fig. 3). Small numbers of young were trapped at the lake outlet starting in mid-August
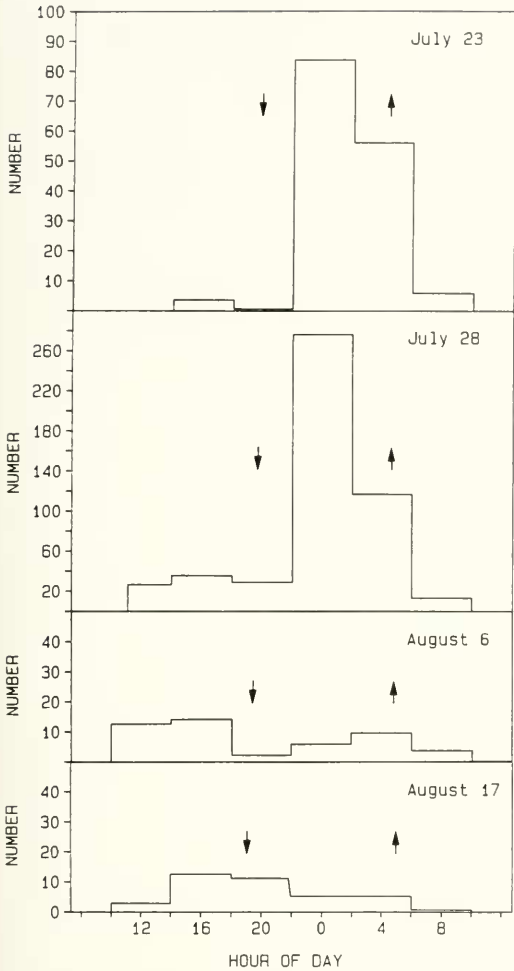
Fig. 2. Diel pattern of young Arctic grayling (*Thymallus arcticus*) accumulated in waterfall trap during 3- or 4-h sampling periods (1000 or 1100 h to 1400 h, then at 4-h intervals thereafter), Deer Creek, Montana, 1990. Note change of y-axis on July 28. Mean sizes of young on these sampling dates are in Figure 3. Arrows indicate sunset and sunrise.

Fig. 3. Mean daily temperature (°C) of Deer Creek, Montana, mean total lengths of age-0 grayling (*Thymallus arcticus*) in waterfall and lake traps, and numbers of age-0 grayling in the lake trap, 1989 and 1990. Arrows indicate dates when numbers of young becoming free-swimming (collected in emergence traps) peaked during 1989 and 1990.

1989 and early September 1990. Total numbers of young trapped per 3-day to 1-week periods in September and October were 0–26 in 1989 and 0–14 in 1990 (Fig. 3). Only 95 age-0 young had moved up into the lake in 1989 and 23 in 1990, before observations were terminated by the onset of winterlike conditions in November 1989 and October 1990. While age-0 grayling in the falls trap were mostly newly swimming fry that averaged 12–14 mm in length, the smallest moving upstream into the lake trap averaged 52–54 mm in length (Fig. 3).
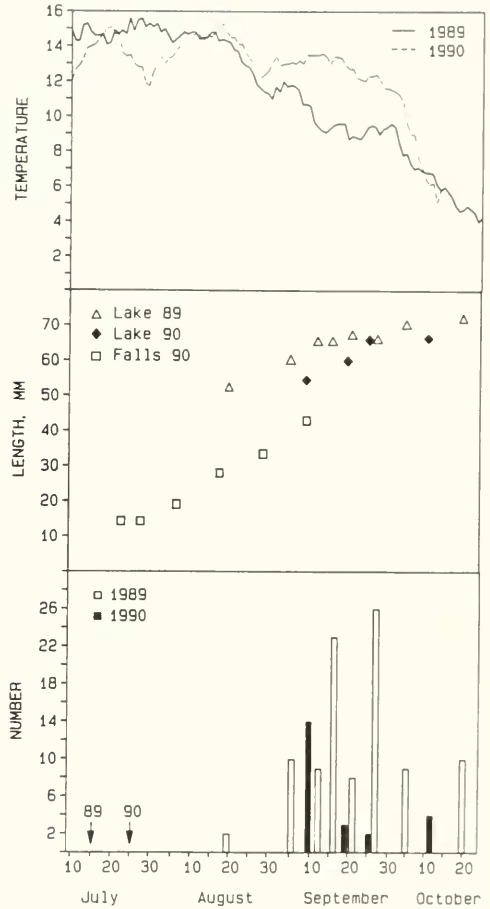
Although numbers of resident young in the stream were not estimated, visual observations indicated that age-0 fish were abundant in November 1989 as ice was starting to form on the stream, but were present in much fewer numbers (as age-1 fish) when ice cover melted the following June. The age-1 fish still in the stream in June 1989 and 1990 had upstream patterns of movement similar to those of the age-0 fish; very few entered the lake during the June–November study period, and these limited upstream movements occurred mostly

between early September and the end of observations in October or November. In 1989 only seven age-1 fish were in the lake trap from June to the end of August, and 38 more from September to the end of observations in November. In 1990 only two age-1 fish were trapped, both in September. Age-1 fish were nearly absent from the falls trap; three were trapped in 1989 and two in 1990. Fish older than age-1 were rare in the stream when ice cover thawed in June of both years.

During the summer of 1990, six adults remained in the outlet stream. These fish were seen in shallow water (5–10 cm deep) chasing groups of young in late July. One was captured with a dip net and had 12 age-0 grayling in its stomach.

DISCUSSION

Since we did not estimate the number of young produced in the stream, we do not know the percentage of total young lost over the falls between swimup and the end of observations in October and November. Two considerations suggest that the losses represented a relatively small percentage of young produced. First, it was visually apparent that age-0 young remained abundant and widely distributed throughout the stream until the end of each observation season. Second, we estimated that the number of eggs that could have been spawned by this population during 1989 was about 1.3 million. This was based on the estimated average of 2988 eggs in each of seven females sampled (range 2459–3674) and the estimated number of 426 adult females in 1989 (Deleray 1991). If we assume, as an example, that swimup fry resulted from 10% of this potential egg deposition, then the estimated loss of young over the falls (5000–9000) would be about 4–7% of fry produced in 1989. We do not know of any estimates of the relationship between potential egg deposition and actual fry production by grayling. However, a figure of 10% seems conservative compared with recent estimates of 11.5–22.2% for chum salmon (*Oncorhynchus keta*) and 16.4–29.1% for coho salmon (*O. kisutch*) in a Canadian stream, with the lower percentages associated with poor substrate quality (Scrivener and Brownlee 1989).

The grayling lost downstream were predominantly small, newly swimming fry that went over the falls at night. The nocturnal down-

stream movement of the young was similar to those of young from inlet-spawning populations of grayling (Kruse 1959, Lund 1974, Wells 1976) and other salmonids (McCart 1967, Northcote 1969, Brannon 1972). These observations were also consistent with results of experiments in an artificial stream (Kaya 1989), which indicated that although young Deer Lake grayling had an innately greater tendency to swim upstream than those of an inlet-spawning population, many moved downstream, especially in darkness.

If loss over the falls results from deliberate downstream migration by the young, then this may indicate that the Deer Lake population has not yet completely adapted to outlet spawning. If so, then the waterfall is continuing to act as a selective factor removing those young with inappropriate responses. Incomplete adaptation has also been suggested as an explanation for downstream movement by many swimup fry of rainbow–cutthroat hybrid trout that spawn in the outlet of a Colorado lake (Lentsch 1985). The lake had first been planted with trout about 100 years earlier. Little or no downstream loss has been reported from populations of brown and rainbow trout native to waters above falls (Northcote 1969, 1981, Jonsson 1982, Northcote and Hartman 1988), in contrast to downstream movement over cascades of an estimated 22% of marked rainbow trout in a stream that had been stocked repeatedly in preceding years with nonnative rainbow trout (Chapman and May 1986). The Deer Lake population almost certainly originated through a transplant of young from an inlet-spawning population sometime during the present century. In Montana, grayling were not present above natural barriers to upstream movement, and the only lakes within the original range that were naturally accessible to fish and known to have contained native grayling were Upper and Lower Red Rock lakes and perhaps Elk Lake, of the Red Rock River drainage (Nelson 1954, Vincent 1962). Another lacustrine population originated with the creation of Ennis Reservoir on the Madison River, which contained native grayling. The Red Rock, Elk, and Ennis populations are inlet-spawning. Populations in other lakes originated through stockings that began after artificial culture of the species was initiated in 1898 (Henshall 1906). Unpublished records of regional, state, and federal hatcheries involved in these stocking programs indicate that fertilized eggs were obtained from Upper Red Rock

Lake or Ennis Reservoir or other inlet-spawning populations established through transplants from these two sources (Kaya 1989, 1990). Outlet-spawning populations are known to have evolved elsewhere from transplants of inlet-spawning grayling (Kruse 1959) and rainbow trout (Northcote 1969).

It is possible that downstream loss of many young fish occurs even from populations well adapted to spawning above a waterfall. With native, above-falls populations that have been studied, the young sampled were brown trout from about 10 cm to over 20 cm in length (Jonsson 1982), or rainbow and cutthroat trout whose sizes were not stated (Northcote 1969, 1981, Northcote and Hartman 1988). Given the rapid post-swimup decline of downstream movement observed in the present study, conclusions on magnitude of such losses would have been very different if the sampling had begun one or two weeks after the end of the swimup period, or if the only fish sampled were larger than 1.5–2.0 cm.

Factors other than deliberate downstream movement could have produced losses over the falls, including passive drift or local dispersal. Those young that were lost could have originated from eggs either spawned within or drifted to locations close to the falls. Adults spawned within 15–20 m above the falls, and we confirmed visually that many eggs drift downstream from spawning areas after being broadcast over the substrate. Fry originating from eggs near the falls could be lost through passive drift if they became free-swimming at night and were consequently displaced downstream in the darkness, as has been described of European grayling (*T. thymallus*; Bardonnet and Gaudin 1990). Downstream losses could also represent passive drift of dead or unhealthy fish, as suggested by a report that 81% of young brown trout produced in a section of stream did not survive and drifted downstream, mostly at night (Elliott 1986). We did not attempt to determine the health of young grayling in the falls trap.

Loss over the falls could be an indirect consequence of local dispersal of young within the stream as they became free-swimming. Young sockeye salmon (*Oncorhynchus nerka*) of outlet-spawning populations have been reported to temporarily disperse downstream before holding position or swimming upstream into lakes (McCart 1967, Brannon 1972). Young grayling in Deer Dreek also disperse locally

from the immediate spawning areas, some of them apparently downstream. For those becoming free-swimming near the falls, even localized downstream dispersal could result in some being carried over, especially under conditions of poor visibility at night.

The results indicate that Deer Lake grayling spend at least the first, and possibly also their second, summer and early to mid-autumn in the outlet stream. However, the results did not permit us to determine the exact timing of most movement by young into the lake, or whether they move upstream predominantly as age-0 or as age-1 fish. The very few young that moved into the lake during both observation seasons could not account for the numbers of spawning adults produced in the population. Since there is no other source of young, and since the 1989 observation season extended over the entire ice-free period on the stream, maintenance of the Deer Lake population must depend on upstream movement of young sometime during the six to seven months of annual ice cover. Although age-0 young greatly diminished in numbers and age-1 fish virtually disappeared from the stream between the onset of ice cover in November 1989 and its thawing in June 1990, we do not know the proportions of these reductions in numbers attributable to movement into the lake, death, or loss over the falls. The greatly diminished numbers of young in the falls trap during late summer and their absence in the trap by October of both years suggest that downstream losses during winter may be small. The chronology of major movement by young grayling into the lake and the numbers and ages of fish involved would need to be resolved by observations during winter.

Little is known about duration of stream residence for outlet-spawning populations of Arctic grayling. Young from inlet-spawning populations of the species typically have an early descent to the lake, ranging from immediately after swimup (Kruse 1959, Lund 1974, Wells 1976) to within several weeks (Nelson 1954). We are not aware of other studies on stream residence times of young grayling from outlet-spawning populations and so do not know whether extended period of stream residence is typical for such populations. Young rainbow trout of outlet-spawning populations tend to remain for extended periods of at least a month to a year or more before migrating upstream to lakes, while those of inlet-spawning populations

migrate when newly swimming in some populations and after extended periods of stream residence in others (Northcote 1969). The extended stream residence of young Deer Lake grayling is also consistent with their lesser tendency to swim upstream in an artificial stream as early fry (from swimup to three weeks), compared with their responses when older, within a study period of up to 10 weeks post-swimup (Kaya 1989, 1991).

It may be that young of an outlet-spawning population need to attain larger sizes and thereby become stronger swimmers before they can swim upstream into the lake. However, this possibility appears contradicted by our casual observations that age-0 grayling of all sizes in Deer Creek, starting from those newly swimming, were capable of swimming upstream when they were disturbed by our presence. Those young originating from spawning areas within a few meters of the lake outlet could have entered the lake by moving only a short distance upstream.

Another possible factor, quality of rearing habitat, also does not appear to favor extended residence in Deer Creek. Deer Lake grayling grow slower during their first two years than those of other lacustrine populations studied thus far in Montana, but thereafter they grow at similar or faster rates (Deleray 1991). Unlike young Deer Lake grayling, those from inlet-spawning populations in Montana spend their first summer and autumn growing season in lakes. The slower early growth of Deer Lake grayling thus appears related to their spending their first growing seasons in the stream rather than in the lake.

We speculate that young Deer Lake grayling may remain in the outlet stream to avoid intraspecific predation in the lake. Eriksen (1975) observed that age-0 grayling in several Montana lakes occupied shallow, near-shore areas among rooted aquatic vegetation, and suggested that their distribution provided protection against predation by the adults. Behavior of the few post-spawning adults that remained in Deer Creek during the summer of 1990 confirmed that adults will prey on the young. Young grayling would likely be susceptible to predation by larger conspecifics in Deer Lake because of its high water clarity throughout the summer and the lack of rooted macrophytes. In the outlet stream the only potential predators of young grayling that we saw were the relatively few residual adult and age-1 grayling remaining through the summer, and an occasional belted kingfisher (Aves, *Ceryle alcyon*). Thus, the movements of age-0 Deer Lake grayling that remain in the outlet stream appear adapted both to beginning their existence a short distance above a waterfall and to avoidance of predation by larger conspecifics in the lake.

ACKNOWLEDGMENTS

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